UNCLASSIFIED

AD NUMBER
AD838471
NEW LIMITATION CHANGE
TO **Approved for public release, distribution unlimited**
FROM **Distribution authorized to U.S. Gov't. agencies and their contractors; Critical Technology; APR 1966. Other requests shall be referred to Department of the Army, Fort Detrick, MD.**
AUTHORITY
SMUFD ltr, 14 Feb 1972

THIS PAGE IS UNCLASSIFIED

TRANSLATION NO. 1652

~~NO. 13~~

DATE: Apr. 1 1966

AD838471

DDC AVAILABILITY NOTICE

Reproduction of this publication in whole or in part is prohibited. However, DDC is authorized to reproduce the publication for United States Government purposes.

STATEMENT #2 UNCLASSIFIED
This document is subject to special export controls and each transmittal to foreign governments or foreign nationals may be made only with prior approval of Dept. of Army, Fort Detrick, ATTN: Technical Release Branch/ TID, Frederick, Maryland 21701

DEPARTMENT OF THE ARMY
Fort Detrick
Frederick, Maryland

8

1652

ON THE ANATOMICAL CHANGES OF THE LEAF-JOINT, WHICH LEADS TO ABSCISSION OF THE LEAVES

(Following is the translation of an article by Hugo V. Mohl, Tubingen, Botanische Zeitung, (Botanical News), No. 1, January 6, 1860, pages 1-11. Translation performed by Constance L. Lust.)

This year in the fall for the first time in many years I was able to duplicate the conditions of abscission of leaves. I was able to study the organic changes in several plants. There are few phenomena, which excites such interest and which should lend themselves to thorough investigations, as the yearly, repetitive defoliation of our trees. There has been no shortage of studies, but, as we shall see, they were all rather far removed from the truly important factors responsible for this process. I, myself had earlier made observations about these events, but they were few and not always on the same plants for any significant length of time. Therefore, I had no clear-cut outlook about the changes that occurred, and were responsible for cessation of activity in the joint of the leaves. This year fall (autumn) was favorable for these studies because the weather was milder than usual in our area. Only on the night of 22 October did it freeze. This allowed me to investigate the changes in a large number of plants. I observed how they release the leaves after slowly dying off. I am still far from considering the present work as complete; this would take much more extensive investigations which would require many years of additional work.

These studies are more time consuming than it would at first appear, because a large number of plants have to be looked at thoroughly in the area of the joint. This takes the greater part of a whole year if one wants to extend the studies to year-around green plants or gray plants. I have thus far not done this, but I restricted myself to observing summer-green plants and wood-plants that live in our area, during September, October and the beginning of November. In this way I have undoubtatly missed a number of modifications that may occur, and likewise I did not follow the analogous situation which occurrs in the abscission of blossoms and blossom-organs which bear fruit. Therefore I ask that this work be considered as a preliminary study (a partial resolution) of this extensive area. More work is required and I will study these problems further if there is time and opportunity.

It may be of use to describe (in a forward) the basic principles which are thought to lead to abscission of leaves.

The first investigators in this area, trying to explain leaf abscission, thought to explain it on a purely mechanical principle. Above all, Duhamel (Physique des arbres I. 129) should be mentioned. He assumed

that a tissue layer was formed between the stem and the leaf (similar to, as between internodes of grape plants) which could not withstand the cold of the winter. Duhamel, however, did not feel that this explanation would be valid for all cases. It was known that leaves that only develop toward autumn can withstand cold better than those that develop in the spring. Further leaves also fall off in frost-free climate and in green houses. Therefore another explanation must be forthcoming to account for this. ~~He was~~ convinced that a second cause of leaf abscission must be present, and ~~he thought it~~ probable that leaves stop growing because of water evaporation, whereas the stem continues to thicken which caused a mechanical mismatch between the leaf and the stem. This then would rupture the fiber which connects the stem and leaf. Du Petit Thouars (Histoire d'un morceau de bois 136) later also brought forth a similar hypothesis, based on rupture of vessels of the leaf. Correctly, this hypothesis did not receive further recognition in scientific circles, because the assumption of rupture of leaf fibers is in direct opposition to all results of anatomical investigations.

If Duhamel believed that the first change responsible for abscission of leaves was the enlargement of stem which led to a curtailment of liquid flow; then Mustel (Traite de la vegetation I. 109) believed, on the other hand, that the cause was an overfilling of the leaf with juices. He felt strongly that it was an incorrect assumption that leaves fall off in autumn because of lack of liquid; therefore dry up, die and fall. He claimed that instead the leaves are overfilled with juices because they have stopped enlarging.

If the juices on the stem and subjected to heat from sun light in the fall and in this way expand, then the juice cannot get into the leaf, and it would press so hard against the stem that this would release. As curious as this proposal is, and even if it has no true basis and does not serve as a solid basis for abscission of leaves, it was nevertheless based on a valid observation. As Mustel stated, the observation that the stem of the leaves falling in autumn is thoroughly filled with liquid in the area where abscission occurs. It is quite correct that the cells of the joints are filled with liquid and that a drying-up of this area does not occur at the time the leaf falls.

An even more unfortunate thought than Mustel was brought forth by Murray (Opuscula L. 138). This author assumed that the pressure in the bud of the stem would draw the liquid toward it and in this way cause the leaf to die and subsequently fall off. This hypothesis is undoubtedly all wrong. The small leaves of a larger leaf (common stem) release themselves in the identical manner as does the main leaf.

A totally different hypothesis was offered to the science of leaf abscission by Gerard Vrolik (Dissert. de defoliatione vegetabilium 1796). This was based on sound physiological principles. He reasoned that tissue-life cannot be added on piece by piece, but represents a compilation

of several constituent parts. He likened it to a machine, where the life of the whole must be the total summation of all the smaller organic constituents combined. Every organic constituent is alive in itself and has its own life-span. For this reason the various parts of the whole can run their own ways in seemingly different individual paths. Plants offer a number of good examples of this; the core dies at one point in time, and the other parts of the growing.organ continue, while the outer layers are still strong. In this way every leaf leads its own life and die at a specific time, independently of the duration of life of the other parts. Vrolik further adds that leaves fall off and the reason for their death may be natural causes, or they may die early because of the effects of excessive heat, or cold, or through illness. The abscission of the dead leaves Vrolik does not explain by means of mechanical causes, but he believed that a layer was formed between the living and dead part of the plant which separates the two and thus causes abscission. This layer is absorbed first in the tissue cells and later in the vessel fibers of the joint of the leaf.

The demonstration that leaf abscission is not caused by a mechanical stimulus, but is due to the death of the leaf, has been generally accepted as a basic truth since Vrolik described this phenomena so lucidly and convincingly. However, his claim that the separation is caused by an absorption of a tissue layer was not based on accurate microscopic measurements or other thorough investigations, but was arrived at by analogy of this process with similar phenomena in animal bodies. In this regard Vrolik's teachings about leaf abscission contained an important omission. To fill in these details was left to his successors. It had to be determined whether during abscission a tissue layer was absorbed in the leaf joint area, and its manner of absorption had to be known. It could still have been possible that abscission of leaves is dependent on still another mechanism. Therefore the attention of the successors was turned to an anatomical investigation of the leaf joint. The investigation yielded results in two sub groups. One group of data -the majority- pointed to the concept that in the original synthesis of the leaf joint pecularities of structure were built in, which lead to abscission after the leaf's death. This concept for which this is the basis is actually a step fack from Vrolis's point of view. The abscission of the leaf was not caused by a structure present already, but because that only in the time immediately before the leaf falls off, after its death, a.special structure is formed in the joint independently, which then effects abscission (release). Few investigators agreed fully with Vrolik on this point (based on their own studies), but I believe that none followed the whole process adequately.

Vaucher is among the investigators who looked for the origin of abscission in the structure of the leaf stem. The basic facts of his view had already been published by Senebier (Physiol. veget. IV. 253). Vaucher himself only published in 1821 (Memoir. d. la societe d. phys. et d'hist. natur. d. Geneve I. 120). This work, however is unfortunate, because the results presented were not in line with the anatomical data about the specific structure of the leaf joint. According to Vaucher

implication of a parenchyma layer was found between stem and leaf-stem. The layer was tightly held to the two organs as long as it remained moist, but it fell when it dried, or changed, the binding was broken. He also thought that the fibers of the stem (main stem) and the stem of the leaf did not go continuously from one into the other, but that they were bound together in some way inside the parenchyma layer. Therefore if the fibers of the stem of the leaf die, and those of the main stem live, a separation would occur between the two. According to the present state of plant-anatomy it is superfluous to try to demonstrate all these assumptions.

Schultz also presented an explanation that was rather arbitrary (Natur d. leb. Pflanze I. 248). According to this author the individual vessel fibers are situated at the site where abscission will occur on the leaf stem. The fibers separate from each other so that no more liquid can reach the leaf through the stem. The abscission surface eventually becomes a scar. The way in which the dividing actually takes place is not discussed by the author. It is really superfluous to discuss the anatomical discription, since this is adequately known by workers in the area. It is known that the vessel fibers close up in the initial stage of growth and they disappear later. Some people still feel it may be the reverse situation.

Schultz postulates that the dividing is dependent on organic alterations in the vessels. Other authors feel that the answer is to be found in specific behavior of the tissues of the leaf joint. Link wrote (Bemerk. u.Zusatze zu Sprengel's Werk ub. d. Bau u. d. Natur d. Gewachse 51) that tissue-structures do not extend unbroken into the stem of the leaf. The cells exist in rows which appear to extend into one direction, but not very far, then they turn back in the original direction. In these cells that change their direction is where abscission always takes place. Link does not give a more detailed explanation of the dividing process. I believe his claims about this cell layer is too general as will come out from the discussion to follow below.

De Candolle (Organogr. I. 133) who put forth a similar proposal about the structure of the joint, believed that a row of cells lying in a plane dry up, or otherwise separate from surrounding cells, whereupon the fibers that are still connected break apart. I will show below that in reality a drying-out does not occur.

Treviranus (Physiol. I. 435, II. 216) also believed that the cell structures of the joint were always heterogeneous; of a different form, size and extended in different directions. He believed that when cells died a "backing-up" of tissue fluids occurred and the cells could not adhere to each other any longer. This of course resulted in separation. The evidence to be presented below will demonstrate that even in these claims the most important aspect was overlooked.

In contrast to the above investigators Schact (Anatom. u. Physiol. II. 136) sought the explanation for the separation and falling of leaves not in the peculiarities of those leaf joint which were already present long before abscission, but in an alteration of the structure of those which are formed relatively later. He claimed that a cork-layer was formed in the joint which stopped the exchange of fluids between stem and leaf. He believed that the formation of the cork-layer may be a cause which eventually is responsible for the leaf's death. Or, more likely, that the cork-layer is of benefit to branch rather than the leaf. The anatomical claim, a building of a periderma, is correct for several woody plants. But this periderma is missing as often as it is present. However he does not explain the dropping off of leaves. The real cause of the latter was completely overlooked by Schact.

The only real investigations were done by Mettenius. He presented his results in a very short report. He reports (Filices hort. botan. Lipsiensis 18), that in those ferns, which release their leaves, the process is initiated and made possible by the death of a soft-walled parenchyma layer which is formed, as in dicotyles, between the leaf and the stem of the leaf. This completes the list of the work known to me. One more report is still worth mentioning. Treviranus wrote to me about a short report by Inman (Proceed. Leverp. Philosp. Soc. IV). It is reported here that the cell structure (tissue) which effects the abscission of the leaf from the stem grows stronger and in this way loosens the cells surrounding it. Finally it breaks. I was not able to read this article myself, and do not know any more about it. I wrote my article (present one) for the German community and probably few German botanists will get to see the Inman article. If his conclusions are similar to mine, it would be fortuitous because I had written my report before I received the note about his work.

After this critical discussion of the views of my predecessors I shall now procede to report my own observations.

In order to obtain a good insight into the anatomical conditions of the"insertion position" of the leaf, which is ultimately responsible for the leaf's abscission, it is most useful to investigate the most complicated first. In those cases the tissue layers are clearly formed, and are separated from each other. For these investigations the large leaf pads of Ailantus glandulosa, Gymnocladus canadensis, Robinia, Gleditschia, etc. are especially convenient.

I will not adhere to the kn wn color alterations, as is generally known to occur in leaves that . to fall off. To be sure this occurs early, long before most leaves ... ready to fall; a decrease in the fluid content of the leaves is also known to occur at this time. In plants like Catalpa syringaefolia this results in a shrinking of the lamina, and in large plants in a dehydration of the inside tissues of the plant organs. Sometimes the stem shrinks as does the upper expanded part of the leaf. On the other hand fluid drips from the bark of branches often obviously at this time. The lower part of the leaf does not participate

in this dehydration. The abscission surface (cut) later passes directly through the middle of this tissue. The cut appears slowly and in part "partially broken up", so that a part of the parenchyma is already completely separated, while other portions are still firmly attached. It's further known that the cut at first only reaches the tissue of the joint, and that the vascular fibers can still be connected between leaf and branch. Of course, a weak external force can cause this to split apart and fall off. The point at which the cut appears is apparent as a line in most plants but not in all. The periderma of the branch borders against the green stem of the leaves. In many cases the cut starts higher on the stem, so that a part of the leaf remains in contact with the twig.

In order to elucidate the special anatomical conditions of the leaf joints, as they appear at the time of abscission, it may be of value to describe the observations found with Gymnocladus canadensis during the period of 10-20 October. During this period many leaves released their pinnate leaves and on the common stem buds also fell off toward the lower part of the plant. Below the stem-swelling the green bark of the branch continued uninterrupted over the outer woody surface. The cells in the green rind contained many starch granules. The periderma of the twig surrounded the base of the stem. Right above the green rind, a completely formed layer of the cells formed in squares and was 1/20" thick. This was the peridema, which continued into the inner layers of the twig epidermis. This periderma forms a distinct separation between the rind and the stem of the leaf. The cells of the stem separate in the area of this peridermal layer. The cells of the stem "swelling" contain almost no chlorophyll compared to the cells of the green rind. Above this cells are found with a small quantity of green pigment. The periderma is next to a layer colored brown. When these cell membranes are brown the cells are undoubtatly on their way to falling off. This brown cell-layer is not clearly separated from the adjacent clear cells. I will call this layer the "round-celled layer" because the cells are shorter than in the rind or stem. The brown layer is not a smooth surface, but rather is much thicker, because of vascular bundles in this area. This results in forming small hill-like structures in the area of the bundles.

Parallel to this layer a thin cell layer is found along the whole width of the previous band to which we must give special attention. If one looks at a leaf which is about to fall, but has not cut yet, then this layer can be seen. It appears more transparent than the other tissues because it contains less air in the intercellular spaces. Treatment with an iodine tincture shows a large number of small starch granules, (which are not found in the rest of the stem swelling) as well as a high protein content. This reagent also causes aggregation of other small particles something that does not occur in other surrounding tissues. All these phenomena pointed to the fact that this layer exhibits all the characteristics of a young tissue, and that it is the locus of an important vegetative process. Many thin "separation walls" can be seen in this tissue upon closer examination. There can be no doubt that cells are multiplying in this layer. If a leaf that just fell is studied one

sees that the cut is derived from the cell layer containing the large quantity of starch.

Both sides of the cut is lined with "rounded off" cells. This cell layer I will refer to as the "dividing layer" or "abscission layer". This layer does not run exactly parallel to the brown, round celled layer. After the leaves have falled off the leaf-scar is not formed from the brown cell layer, but rather from the non-colored cells of the stem swelling. This, of course, drys very rapidly after exposure to the air.

The dividing layer is only formed shortly before abscission occurs. In Gymnocladus it had not been formed on October 4. At this time the periderma and the rounded off cell layer were already present. The synthesis of the dividing layer did not occur simultaneously along the cross-cut of the stem, but rather proceeded from the inside. Therefore, it is not uncommon in these leaves that division is complete internally, while the outer portion of the stem is still bound to the bark.

I cannot say at what time the internal periderma is formed, because I started in mid-September and at this time it was already formed.

The vascular bundles apparently take no part which results in abscission in the alteration of the tissue of the stem. The bundles run all through these tissue layers without changing their organization. The cut through the bundles, after the cut through the tissue, is merely mechanical. This aspect of the work has already been published (Botan. Zeit. 1949) p. 642)

(To be concluded)